ON THE MALE GAMETOPHYTE OF PICEA CANADENSIS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 200

A. H. HUTCHINSON

(WITH PLATES XV–XIX AND ONE FIGURE)

The male gametophyte of *Picea excelsa* has been described by STRASBURGER, MIYAKE, and POLLOCK. At the shedding stage, as recorded by STRASBURGER (1), there are two disintegrating prothallial cells, a stalk cell, a body cell, and a tube nucleus. MIYAKE (2) verified this account; also described the pollen tube stages and the division of the antheridial cell into stalk and body cells. POLLOCK (3) noted certain variations in the gametophyte at the time of pollination. This account deals with the early stages of development in the male gametophyte of *Picea canadensis*.

The staminate cones were collected from trees growing near Lake Simcoe, Ontario, Canada. Daily collections were made from May 2 until May 15, the time of shedding. The usual time for pollination in this locality is about two weeks later.

Nomenclature

The nomenclature used in accounts of male gametophytes has varied according to the character used as a basis for the system, whether it be size, position, or the writer's conception of origin or function of the different cells. Early in the nineteenth century FITZSCHE described *Pinus* as having a large central vesicle and disintegrating bodies against the wall of the pollen grain (*Zwischenkorper*). MEYEN (in 1839) stated that the *Zwischenkorper* were cells, and that one of them served as a stalk of attachment. JURANYI (4) reported that in *Ceratozamia* the pollen mother cell divided into a large and a small daughter cell (*kleine Tochterzelle*); that the latter divided to form two, and that the inner of these gave rise by division to an inner cell and an end cell. These three cells were collectively known as the cell body (*Zellkörper*). Until 1891 the tube nucleus (*grosse Zelle* or *freigebildete Zelle*) was believed

to be the fertilization nucleus. At that time BELAJEFF (6) showed that in *Taxus baccata* the larger cell is not the generative cell; but that the small cell divides in the tube and one of the derivatives becomes the generative cell.

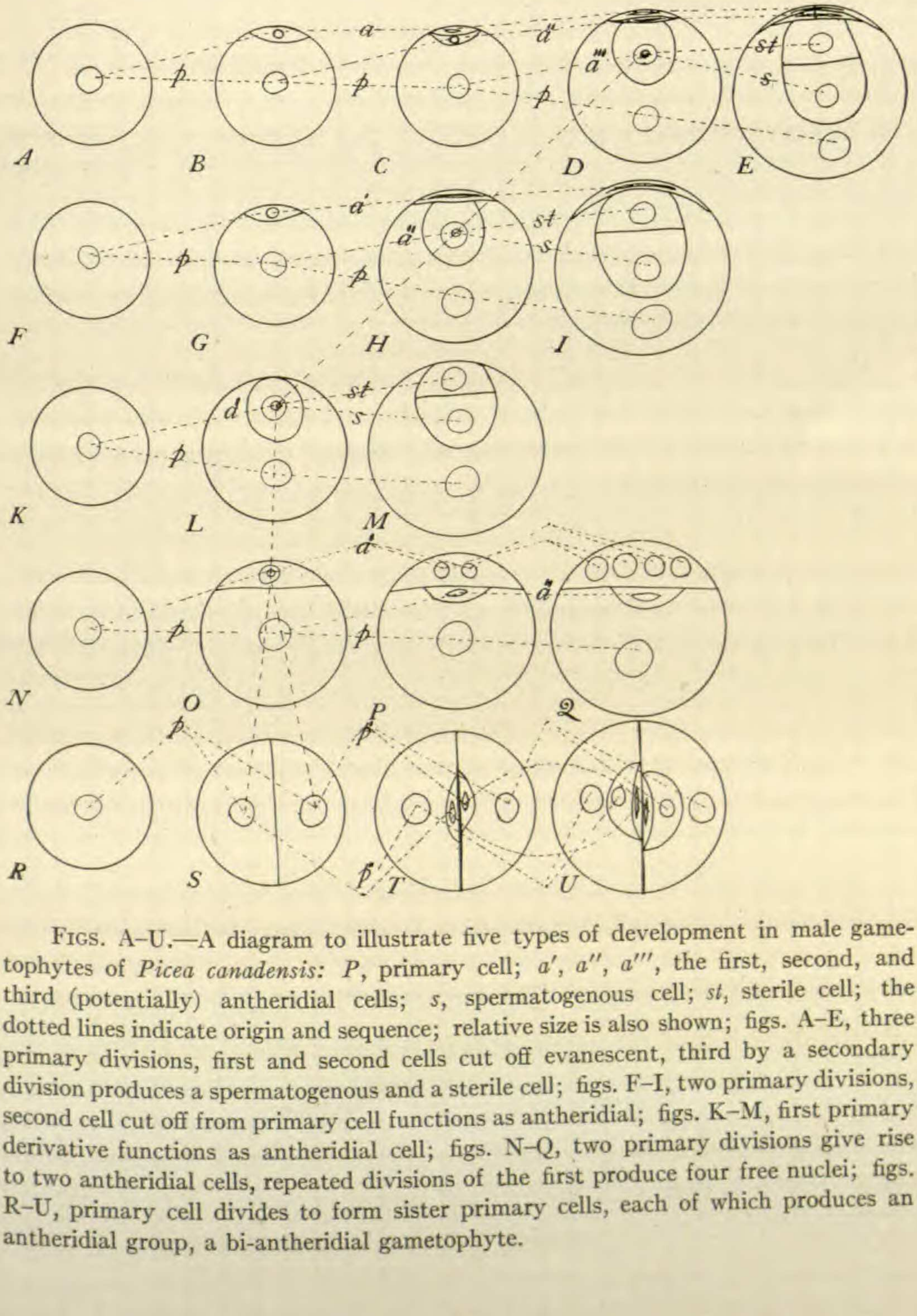
In 1892 STRASBURGER (1) described *Ginkgo biloba* as having two prothallial cells, representing a vegetative prothallus, and an antheridial cell, which are successively cut off from the pollen cell; the antheridial cell divides into stalk and body; the latter produces the sperms. The large pollen nucleus, because of its foremost position in the tube, was called the tube nucleus. The general conception of origin and function is the same today. It is not surprising, however, that, with such a variety of types, different investigators have since used different terms to designate similar cells.

The system of nomenclature to be used in this account has been made necessary by the nature of the gametophytic development. The primary cell (*P*) is regarded as retaining its identity, just as an apical cell. In the pollen tube stages it is represented by the tube nucleus. The successive divisions of the primary nucleus are known as primary divisions; the cells cut off are called, tentatively, the first, second, or third primary derivatives (a', a'', a''' in figs.). Divisions of the latter cells are called secondary. The cell which later divides to form male nuclei is termed spermatogenous (*s* in figs.); the sister non-functioning cell is the sterile cell (*st* in figs.). The mother cell of a spermatogenous and a sterile cell is called an antheridial cell.

Development of the male gametophyte

The first primary division is variable; the cell wall may cut off a lenticular polar cell (fig. 7); it may be oriented at right angles to the longitudinal axis, cutting off approximately one-third of the protoplasmic mass (figs. 6, 33, 37, 53); it may be in the plane of the vertical axis, in which case two nearly equal cells result (figs. 2, 10, 11, 13, 31, 32); it is often inclined (figs. 28, 29); and occasionally no dividing wall is formed, the two resulting nuclei being then free in the cytoplasmic mass (figs. 8, 9, 12). The further development of the resulting cells is largely determined by the

nature of the first primary division. When the primary derivative is small and lenticular, it rapidly degenerates (figs. A-I and 20–26 etc.); when the division is median or nearly so, each of the two cells formed has the power of repeated division, giving rise to a



FIGS. A–U.—A diagram to illustrate five types of development in male gametophytes of *Picea canadensis*: *P*, primary cell; a', a'', a''', the first, second, and third (potentially) antheridial cells; *s*, spermatogenous cell; *st*, sterile cell; the dotted lines indicate origin and sequence; relative size is also shown; figs. A–E, three primary divisions, first and second cells cut off evanescent, third by a secondary division produces a spermatogenous and a sterile cell; figs. F–I, two primary divisions, second cell cut off from primary cell functions as antheridial; figs. K–M, first primary derivative functions as antheridial cell; figs. N–Q, two primary divisions give rise to two antheridial cells, repeated divisions of the first produce four free nuclei; figs. R–U, primary cell divides to form sister primary cells, each of which produces an antheridial group, a bi-antheridial gametophyte.

so-called double gametophyte (figs. R–U and 28, 29, 31, 32); when the first primary derivative is surrounded by cytoplasm it divides, giving rise to a spermatogenous and a sterile cell (figs. K–M and 9, 12, 30). In this case there is no further division of the primary cell; the first primary derivative becomes the functioning antheridial cell. Again, if the first cell cut off contains sufficient protoplasm it may divide once or even twice to form as many as four free nuclei. When this occurs, the primary cell soon ceases to divide and begins to disintegrate (figs. N–Q and 28, 29, 33). The first primary derivative may function as an antheridial cell by directly dividing to form a spermatogenous and a sterile cell, by repeatedly dividing to form a number of free nuclei, or by becoming primary in nature and hence developing along with its sister cell to form a bi-antheridial gametophyte.

When the first primary cell is evanescent, a second primary division takes place. Nor is it uniform. Frequently the primary cell approaches the first primary wall before dividing, and it may come into contact with this wall. The second primary derivative is then cut off as a lenticular cell against the wall of the first and soon disintegrates (figs. C–E and 23, 25, 26). If, however, it remains imbedded in the cytoplasm of the primary cell, it divides to form a spermatogenous and a sterile cell (figs. F–I and 25, 38). Hence the second primary derivative may function as an antheridial cell.

When, as it has been hitherto described, the first and second primary derivatives are evanescent, a third primary division takes place, and the last cell cut off functions as the antheridial cell (figs. A–E and 42–51).

Since the spermatogenous cell may originate from the first, second, or third primary derivatives, we are forced to the conclusion that these cells are all potentially antheridial, one or in some cases two functioning as such. They may be known as evanescent or functioning antheridial cells, as the case may be.

Development; time; nutrition

Growth is exceedingly rapid; in three days the diameter of the pollen grain is doubled, its volume becoming four times as great. In *Pinus* "the mature pollen grain has the same size and form as

the microspore just prior to germination" (15). When two evanescent cells are cut off, these divisions take place before the increase in size. They follow one another in rapid succession; all stages of the first two primary divisions are to be found in the same sporangium. A resting period, that is, a period during which mitosis ceases, but during which there is a great increase in size and apparently in food supply, precedes the formation of the functioning antheridial cell, whether it be the first, second, or third primary derivative (figs. D, H, L, O, S and 30, 38, 44, 45). Since this last primary division and the secondary division to form the spermatogenous cell and the sister sterile cell are to be found in the same sporangium, it is evident that they are closely consecutive. The complete development is extremely rapid; on May 3 only one-celled stages were to be found, while on May 6, or sooner, the pollination stage had been reached. Trees on a sunny hillside shed the pollen at once; others retained it for ten days without further development. The functioning antheridial cell is imbedded in the cytoplasm of the primary cell, as shown above, and an increase in the size of the pollen grain precedes mitosis of the former cell. Evidently nutrition is a factor in determining the fate of an antheridial cell; in other words, whether the first, second, or third shall function as such.

Degeneration

In lenticular cells which contain a minimum of cytoplasm surrounding the nucleus, the latter does not pass out of telophase (fig. 26); the chromosomes contract, become globular, and finally disintegrate as irregularly granular masses (figs. 20, 21, 43), or accumulate at the periphery of the nucleus, giving it a vaginated appearance (fig. 45). When these cells collapse, double darkly-stained bands appear in cross-section. In *Picea canadensis* the intine does not imbed these degenerating cells. The first primary wall elongates as the pollen grain increases in diameter (figs. 37, 38, 50, 51); often it has the appearance of a third wall (fig. 50) which is attached to the intine near the origin of the wings. The disintegrating cell contents remain within the original walls; the latter meanwhile become elongated and thickened.

Degeneration may occur in any part of the gametophyte. Frequently the second primary derivative degenerates before the first (fig. 37). If sister primary cells are formed, the struggle resulting from their parallel development is generally so great that disorganization of both results (fig. 32). Usually one gains the ascendency. Often, after as many as three cells have been formed, one of the antheridial groups is crowded against the wall; irregular cavities appear in the cytoplasm (fig. 31); the protoplasm contracts and accumulates in masses of globules; and the nuclei becomes massed or uniformly granular (figs. 33, 53). When an extreme development of the first antheridial cell occurs, the primary cell as well as the secondary antheridial cell may disintegrate (fig. 33).

Mitoses

There are two types of mitoses; that characteristic of primary divisions, and that of secondary divisions. The latter does not differ essentially from ordinary somatic mitoses; the former is quite distinctive in its characters.

The nuclei and chromosomes are decidedly kinetic. Just before mitosis, the primary nucleus moves to a more or less polar position. Frequently it comes in contact with one of the primary walls (figs. 14, 15, 16, 43). There is the usual movement of the chromosomes to form the central plate at metaphase, and the separation of chromosome groups during anaphase. After the two nuclei have been formed, the one which is polar retains its position, while the primary nucleus moves to its central or supracentral position (figs. 5–7; 19–25; 43–45).

The changes in the volume of the nuclear space are very marked. During prophase a slight expansion is followed by a contraction (figs. 14, 15, 16, 28) which continues until the disappearance of the nuclear membrane. The chromosomes at the poles during early telophase aggregate into compact masses (figs. 4, 18, 47, 49); the nuclear membrane is formed, and the nucleus expands until it becomes three or four times its original size. There is an associated accumulation or disappearance of food particles in the surrounding protoplasm. This may be regarded as evidence in favor of LAWSON'S (7) explanation of similar phenomena, namely, that they are due

to osmosis. Moreover, the increase in size is most rapid when the nucleus is surrounded by most cytoplasm; the primary nucleus soon regains the size characteristic of the resting stage (figs. 6, 9, 18, 20, 21).

Chromatic structures

The resting nucleus contains several nucleoli. In early prophase "condensing bands" and "zig-zag threads" of chromatin become differentiated; definite looped chromosomes are formed (figs. 15, 35). Only in rare cases could their double nature be seen at this stage; it would seem that the halves remain rather closely appressed until metaphase. The nucleoli are present until late prophase (figs. 16, 35, 48). The chromosomes contract before aggregating in a definite cell plate (figs. 16, 48); during anaphase they are characteristically V-shaped (figs. 2, 3, 17). In early telophase compact chromatic aggregations are formed (figs. 4, 18, 41, 47, 49). These soon become irregularly vacuolate, and as the vacuoles increase in size, anastomosed bands of chromatin become differentiated (figs. 5, 22, 24, 43). The process is similar to that described by SHARP (8) in *Vicia*. The bands become more irregular in outline, and a number of nucleoli appear (figs. 23, 25, 44). As the number of nucleoli decreases, they become individually larger (figs. 20, 45, 6, 8, 46, 48, 50). The irregular bands are replaced by zig-zag threads and the nucleus passes again into the resting condition.

Achromatic structures

The achromatic structures in all primary divisions are most characteristic. The spindle fibers are inconspicuous during anaphase (figs. 2, 3, 36, 42); in many cases they can be distinguished only with difficulty (fig. 17) and are only slightly more definite than the vague radiations in the polar cytoplasm (figs. 3, 36). In early telophase there are very definite strands between the daughter nuclei. These are arranged in the form of a hollow cylinder (figs. 4, 18) which gradually broadens (figs. 19, 43) and moves toward the pole, partly enclosing the antheridial nucleus (figs. 5, 21, 24). Usually the fibers come in contact with the cell wall, the free ends swing outward, and so remain as curved or radiating strands

(figs. 7, 23, 44, 45). The cell plate forms late; it is most definite after the fibers have taken their final position (figs. 6, 7, 8, 41, 45). These mitoses are similar to that described for *Abies balsamea* (9).

The cell plate is evidently associated with the formation of the cell wall. In fig. 45 the arched fibers remain only at one side, but here there is a distinct cell plate and the cell wall is curved outward to meet it. When the wall is formed the fibers disappear. In many cases no cell plate could be seen (figs. 5, 21, 22, 23), and the division in the cytoplasm is continuous with the end of the fibers (fig. 25).

There is abundant evidence that the achromatic fibers are definite structures which change their position. The fact that there are groups of spindle fibers which have no immediate connection with nuclear membranes or chromosomes is further evidence for their individuality (fig. 8).

Secondary divisions have markedly different characters. A polar cap is formed during prophase (fig. 48); the spindle fibers are more strongly developed during metaphase (fig. 38); the cell plate forms early (figs. 47, 49), and the spindle fibers retain their original positions. The similarity of secondary divisions in the first and third primary derivatives is illustrated by figs. 47 and 49.

Chromatic extrusions

In the early stages of the gametophyte, darkly staining bodies occur in the cytoplasm. When the primary nucleus is in the resting stage, these bodies appear as spherical masses surrounded by a clearer area (fig. 34); when the primary cell is in active mitosis these extrusions become fragmented (fig. 35). These bodies originate from wandering chromosomes which escape during mitosis. Separate chromosomes are found near the primary cell wall during metaphase (fig. 36). Evidently these never take part in cell plate formation. They contract into spherical masses and wander into the cytoplasm. In other cases, during late anaphase, several chromosomes prematurely contract to form a more or less compact mass, thereby separating themselves from the chromosomes which later undergo a similar change (fig. 3).

Discussion

1. *Double pollen grains*

There are accounts of double pollen grains occuring in a number of species. Probably first was CHAMBERLAIN'S (10) description of *Lilium tigrinum*. "In about 20 cases there was a distinct wall dividing the microspore into two nearly equal parts." Both cells contained starch. His fig. 20 shows one of the cells containing two nuclei "which seem to represent generative and tube nuclei." One of the cells was regarded as prothallial, the other as antheridial. SCHAFFNER (11) found compound grains where two or more of the spores of a tetrad clung together (*Typha latifolia*). GUIGNARD (12) and Miss PACE (13) figure four microspores of an orchid within a common wall dividing to form tube nuclei and generative cells. COKER (13a) describes double grains in *Larix europea*. His fig. 6 is similar to my fig. 13; his fig. 8 corresponds to my fig. 12. He suggests that "the mother cell had only divided once, so that only two instead of four pollen grains were formed." In some of these grains "division proceeded as usual except that only one prothallial cell is evident" (cf. fig. 32). POLLOCK (3) has described a number of variations in the pollen grain of *Picea excelsa*. "In the material examined, the proportion of double pollen grains was found to be 2.4 per cent in a count of 1120. The three or four cells lying along the dorsal side of the pollen grain of this type do not constitute a prothallium or gametophyte of unusual size. They constitute the smaller portion of a pollen grain separated by a division wall into two nearly equal portions, each of which may form a typical antheridium." Double pollen grains have been variously interpreted. In *Picea canadensis* a study of the stages of development has shown that the two cells from which the double grain arises are the result of a primary division of the microspore (figs. 11, 13), and that one of these cells corresponds in origin to the more usual evanescent cell. All gradations between an equal division and one which cuts off a lenticular evanescent cell have been found (figs. 6, 7, 10, 11, 13). In the double pollen grain of *Picea* one of the antheridial groups is homologous with the usual evanescent polar cell.

2. "*Prothallial cells*"

Several species have been described in which the "prothallial" cell has the power of division. Among the number are *Ginkgo biloba*, by STRASBURGER (1); *Picea excelsa*, by MIYAKE (2) and POLLOCK (3); *Abies balsamea* (9); *Agathis*, by JEFFREY and CHRYSLER (14); *Podocarpus*, by COKER (13a); and *Dacrydium* by Miss YOUNG (16). The similarity of the generative cell and the prothallial cells is pointed out by Miss YOUNG: "In *Dacrydium*, as in *Podocarpus* and *Abietineae*, a third cell is cut off from the main body of the spore. It overlies the others and is so similar to them that, but for its subsequent behavior, one might think it a prothallial cell. It is the generative cell, generative in the sense that it is the ancestor of the spermatogenous cell. This and the second prothallial cell now divide." The first prothallial cell may also divide. Again: "at shedding the pollen grain contains the body cell and five free nuclei. The nucleus of the body cell is indistinguishable from those of the prothallial cells and the tube nucleus." POLLOCK (3) states that in a large proportion of the gametophytes of *Picea excelsa* there is only one prothallial cell. BURLINGAME (20) says: "in *Podocarpus* one primary prothallial cell may be cut off, after which the free nucleus divides to form the free spermatogenous cell and the tube nucleus; or two primary cells may be cut off before the tube nucleus is separated from the primary spermatogenous cell." In these two species, as well as in *Picea canadensis*, the antheridial function is not limited to a definite primary derivative. It has been established that "prothallial cells" and generative cells may be similar in appearance; that frequently they are similar in their power of division; the similarity is further emphasized by the presence of "prothallial cells" in the pollen tube. The present account has emphasized the similarity in the origin, and has shown that potentially there is a similarity in function; that any one or sometimes two of the primary derivatives may be antheridial. To what extent we are justified in suggesting that these phenomena are indicative of a multi-antheridial ancestral form only further research can determine.

Relationships

No one character is sufficient to establish relationships of plant groups. Since similarity of male gametophytes gives only one-sided evidence for the relationship of species or genera, the discussion will be limited to comparison of types. In Taxodineae and Cupressineae the gametophyte consists of an antheridial cell, which may divide before or after shedding, and a tube nucleus; no evanescent cell is present. Similar gametophytes are found in *Picea canadensis* (fig. 30). In cycads two cells are cut off from the primary cell, one of which is antheridial (cf. fig. 38). The shedding stage characteristic of the abietinean gametophyte (also of *Ginkgo* and *Ephedra*) contains two more or less evanescent cells and an antheridial cell, which may or may not divide, beside the tube nucleus (cf. figs. 50, 51, 52). The podocarp type is similar, but the polar cells are not evanescent and frequently divide (cf. figs. 39, 40, 52). A massive polar tissue containing free nuclei, which LOPRIORE (18) regards as antheridial, is characteristic of the araucarian type. A similar gametophyte is shown in fig. 33. The male gametophyte of *Picea canadensis* is in a state of unstable equilibrium. Slight differences in conditions are sufficient to shift the balance in one of several possible directions. The resulting forms correspond to the various types of gametophytes found in gymnosperms.

Summary

In the male gametophyte of *Picea canadensis*, one, two, or three potentially antheridial cells are cut off from the primary cell; one of these divides to form a spermatogenous and a sterile cell; the others, when formed, are more or less evanescent. Occasionally there are two functioning antheridial cells, resulting in a bi-antheridial gametophyte.

The writer is indebted to Professor JOHN M. COULTER, Dr. CHARLES J. CHAMBERLAIN, and Dr. W. J. G. LAND for many suggestions and criticisms.

UNIVERSITY OF CHICAGO

LITERATURE CITED

1. STRASBURGER, ED., Über das Verhalten des Pollens und die Befruchtungsvorange bei den Gymnospermen. 1892.
2. MIYAKE, K., On the development of the sexual organs and fertilization in *Picea excelsa*. Ann. Botany **17**:351–372. 1903.
3. POLLOCK, JAMES B., Variations in the pollen grain of *Picea excelsa*. Amer. Nat. **49**:253–286. 1906.
4. JURANYI, L., Bau und Entwickelung des Pollens bei *Ceratozamia longifolia*. Jahrb. Wiss. Bot. **8**:832–400. 1872.
5. TSCHISTIAKOFF, Beiträge zur Physiologie der Pflanzenzelle. Der Pollen der Coniferen. Bot. Zeit. **33**:86–88, 97–103. 1875.
6. BELAJEFF, W., Zur Lehre von dem Pollenschlauche der Gymnospermen. Ber. Deutsch. Bot. Gesells. **91**:280–286. 1891.

7a. LAWSON, A. A., The phase of the nucleus known as synapsis. Trans. Roy. Soc. Edinb. **47**:591–604. 1912.

7b. ———, Nuclear osmosis as a factor in mitosis. Trans. Roy. Soc. Edinb. **48**:137–161. 1913.

8. SHARP, L. W., Somatic chromosomes in *Vicia*. La Cellule **29**:297–328. 1913.
9. HUTCHINSON, A. H., The male gametophyte of *Abies balsamea*. BOT. GAZ. **57**:148–153. 1914.
10. CHAMBERLAIN, C. J., The pollen grain of *Lilium philadelphicum*. BOT. GAZ. **33**:423–430. 1897.
11. SCHAFFNER, J. H., The development of stamens and carpels of *Typha latifolia*. BOT. GAZ. **24**:93–102. 1897.
12. GUIGNARD, L., Recherches sur la développment de l'anthère et du pollen des Orchidées. Ann. Sci. Nat. Bot. VI. **14**:26–45. 1882.
13. PACE, LULU, The gametophytes of *Calopogon*. BOT. GAZ. **48**:126–137. *pls. 7–9*. 1909.

13a. COKER, W. C., On the spores of certain Coniferae. BOT. GAZ. **38**:206–213. 1904.

13b. COKER, W. C., Notes on the gametophytes and embryo of *Podocarpus*. BOT. GAZ. **33**:89–107. 1900.

14. JEFFREY, E. C., and CHRYSLER, M. A., The microgametophyte of the Podocarpineae. Amer. Nat. **41**:102–107. 1907.
15. FERGUSON, MARGARET C., Contributions to the life history of *Pinus*. Proc. Wash. Acad. Sci. **6**:1–202. 1904.

16a. YOUNG, MARY S., The male gametophyte of *Dacrydium*. BOT. GAZ. **44**:189–196. 1907.

16b. ———, The morphology of the Podocarpineae. BOT. GAZ. **50**:81–100. 1910.

17. CALDWELL, OTIS W., *Microcycas calocoma*. BOT. GAZ. **44**:118–141. 1907.

18. LOPRIORE, G., Über die Vielkornigkeit der Pollenkörner von *Araucaria Bidwillii*. Ber. Deutsch. Bot. Gesells. **23**:235–246. 1905.
19. THOMPSON, R. B., Preliminary note on the Araucarineae. Science N.S. **22**:88. 1905.
20. BURLINGAME, L. L., The staminate cone and male gametophyte of *Podocarpus*. BOT. GAZ. **46**:161–178. 1908.

EXPLANATION OF PLATES XV–XIX

The drawings (figs. 1–53) have been made with the aid of the Abbé camera lucida. The original magnification was 2000. A reduction of one-half has been made in reproduction.

FIGS. 1–13.—The first primary division; the primary cell retains its identity; the first primary wall cuts off an antheridial cell.

FIG. 1.—Primary cell.

FIG. 2.—A division at right angles to the longitudinal axis.

FIG. 3.—A division in the plane of the axis; a chromatic extrusion is being formed and is separating from the nuclear chromosomes.

FIGS. 4, 5.—Telophases: the primary nucleus and spindle fibers separating.

FIGS. 6, 7, 8, 11.—Telophases: each shows the cell plate in one of 4 positions; in fig. 8 both nuclei have escaped from the spindle fibers.

FIGS. 9, 12.—Two free nuclei in common cytoplasm; compare fig. 8.

FIGS. 10, 13.—The primary cell has given rise to two daughter cells, each of which may function as a sister primary cell.

FIGS. 14–27.—The second primary division.

FIG. 14.—The primary cell in contact with the first evanescent antheridial.

FIGS. 15, 16.—Prophases.

FIG. 17.—Anaphase: spindle fibers indistinct.

FIGS. 18–25.—Telophases: illustrate migration of primary nucleus and spindle fibers; fig. 24, a view from upper pole; figs. 23–25, the formation of the cell wall.

FIGS. 26, 27.—Pollen grains with primary cell and two non-functioning antheridial cells; compare size with fig. 1.

FIG. 28.—First antheridial ("prothallial") cell in division.

FIG. 29.—Primary cell; also first and second antheridial cells; the former has divided to form two nuclei.

FIG. 30.—First antheridial cell has divided to form a spermatogenous and sterile cell.

FIGS. 31, 32.—Two sister primary cells (cf. figs. 11 and 13) have given rise to a bi-antheridial gametophyte (disintegration).

FIG. 33.—Four free nuclei, products of first antheridial cell; the primary cell and second antheridial cell disintegrating.

FIGS. 34–36.—Chromatic extrusions.

FIG. 37—The position of the first primary wall and the large polar cavity is to be noted.

FIG. 38.—The second antheridial cell dividing.

FIGS. 39–40.—Laterally placed derivatives of first and second antheridial cells.

FIGS. 41–46.—The third primary division.

FIG. 41.—A polar view.

FIG. 46.—Large primary nucleus (tube nucleus): the third antheridial cell just before mitosis; the second in normal condition except for compression; the first disintegrated.

FIG. 49.—Mitosis in the first antheridial cell (cf. fig. 28).

FIGS. 47, 48, 50, 51.—Division of the third antheridial cell to form a spermatogenous and a sterile cell.

FIG. 52.—Showing polar cells, the products of secondary divisions.

FIG. 53.—Shows disintegrating derivatives of the first antheridial cell; a sterile cell; a spermatogenous cell and the primary nucleus (or tube nucleus).